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Summer Research Project

Tuberculosis Spread in Possum Networks

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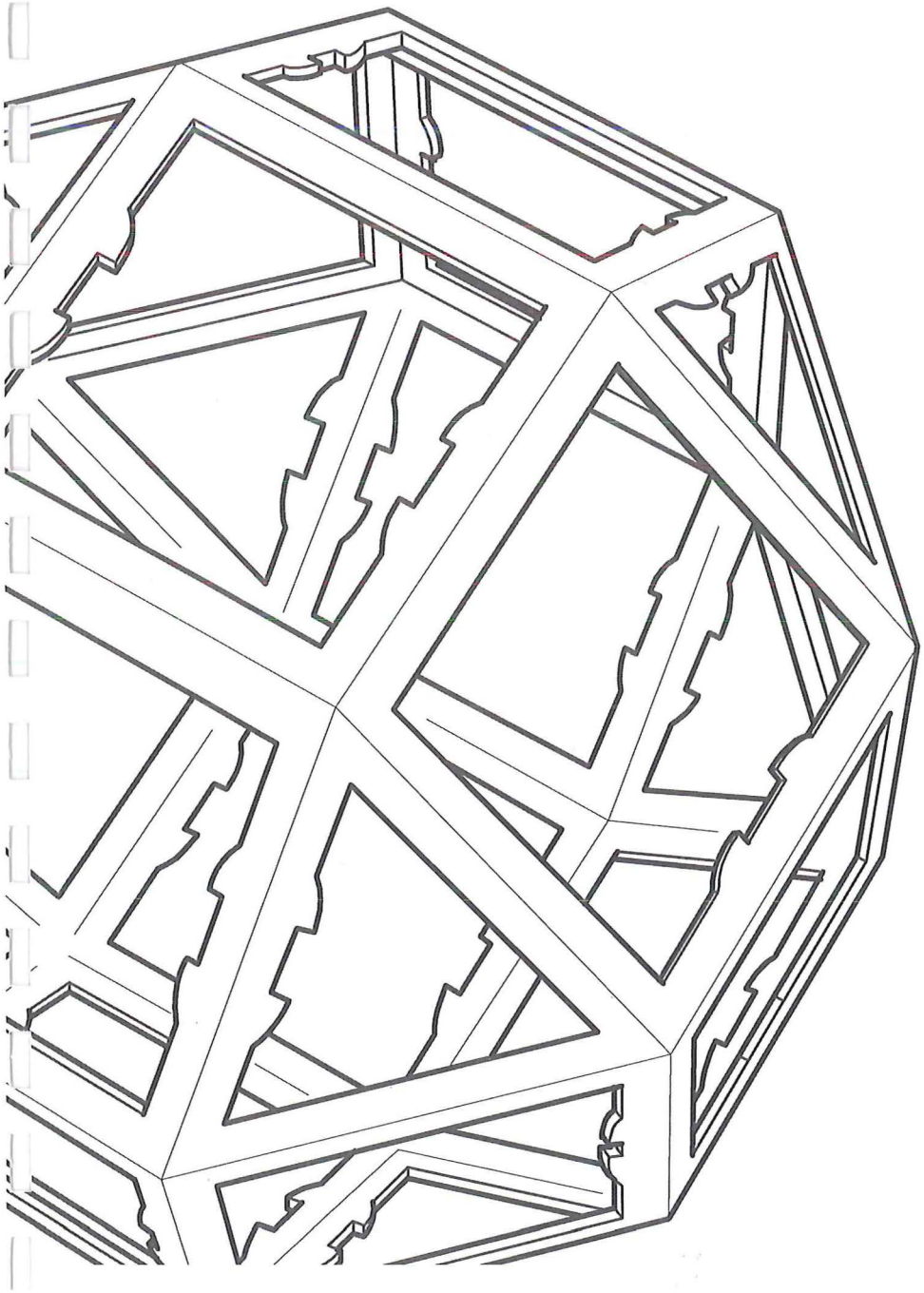

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Tuberculosis Spread in Possum Networks

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Abstract

Since the late 1960's the prevalence of bovine tuberculosis in New Zealand livestock has been associated with nearby possum populations. In order for the disease to be controlled it is important to understand how it is spread between possums. In this report we investigate how certain factors (*e.g.* Death Rate, Meeting Rates, No. of Contacts) impact on how far and how quickly tuberculosis spreads within a modeled network of possums. This gives an indication of which factors are important when dealing with a real population.

1 Introduction

Bovine tuberculosis (Tb) is a fatal disease that affects large numbers of livestock in New Zealand, especially cattle. It causes weight loss and death in both cattle and deer and also remains a minor cause of tuberculosis in humans. It is likely that in the near future, health standards in the meat and dairy industries will be changed to prohibit products containing any pathogen, including tuberculosis (DoC, b). As both of these industries are very valuable in New Zealand, it is important that the problem is controlled as soon as possible. Scientists have linked the high rate of infection in cattle with neighboring possum populations (DoC, b).

The common brushtail possum was introduced to New Zealand in 1837 to establish a fur trade, however their population size has increased so rapidly since then that they are commonly considered a pest (DoC, a). As well as spreading tuberculosis to other species they have also destroyed large amounts of native forest. It is estimated that in New Zealand they consume 21 000 tonnes each night (Hutching, 2009).

Currently in New Zealand several different methods are employed to reduce the possum populations including hunting, trapping and most commonly 1080 bait (sodium fluoroacetate). It is hoped that this will decrease the chances of livestock being exposed to tuberculosis. While the use of 1080 is an extremely effective method of control in terms of reducing possum numbers it also has negative effects on other wildlife where it is distributed, as it is capable of killing other animals including many bird species (Veltman and Westbrooke, 2011).

In order for the spread of tuberculosis to livestock to be controlled it is important to understand how the disease spreads in the local possum populations. In the last 20 years there have been numerous studies conducted looking at this spread and the best ways to control it (*e.g.* Roberts (1996), Corner et al. (2002), Corner et al. (2003)).

Roberts (1996) used a simple model to determine the rates of culling or vaccination that would be required to completely eradicate bovine tuberculosis from possum populations. His results showed that they would need to be culled at a rate of 9.2% per year or vaccinated at a rate of 15% per year. There has been debate about whether his model is appropriate for whole populations or if it is only relevant to small clusters of the disease (Caley, 2006).

Corner et al. (2002) conducted experiments to observe the natural transmission of Tuberculosis between possums. When they mixed infected and susceptible possums randomly they found that transmission rates were extremely low, however when the more socially active possums were chosen to be infected initially, the disease was passed on far more easily. From this they determined that the social habits of different possums should be taken into account when modeling Tuberculosis spread through a population.

Corner et al. (2003) used Social-network analysis to model patterns of denning behavior among closed networks of possums. This was further to their research the previous year. Their results supported their previous research as those possums who shared dens with other possums more often (*i.e.* were more social) were generally the ones who contracted tuberculosis. However, this model only catered for den sharing, which does not cover all social contact between possums.

Tuberculosis is a respiratory disease and is therefore generally transmitted between possums by inhalation of aerosols (Corner et al., 2003). This requires close contact between the possums. The most common methods of direct contact are mating, den sharing and fighting (Porphyre et al., 2008). A five-year capture-mark-recapture study by Porphyre et al. (2008) suggested that on average a possum in the wild will come into contact with another possum 20-26 times per year. Of course this is not expected to be uniform across a network of possums. As with humans there will be variation

in how social different possums are, and we would expect that those that come into contact with other members of the network more often will have a higher change of contracting tuberculosis.

Dr. D.M. Tompkins from Landcare Research has been awarded a Marsden Grant for his research on how diseases emerge, spread and persist. For his model he will use bovine tuberculosis in wild possums. He is going to use 12 networks of 40 possums each, with the aim of determining the impact of 'superspreaders' (very social possums) and 'supershedders' (possums that are very infectious (Tompkins, 2011). For this he needs to have a general idea to begin with about how many possums to infect and how long he will need to observe the populations for. Throughout this report we use a population of 40 possums as Dr. Tompkins will in his experiments.

A commonly used model for epidemic spread in a population is the SIR model. This is a compartmental ODE model first used by Kermack and McKendrick in 1927 (Diekmann and Heesterbeek, 2000). It splits the population (N) into three categories: Those that are susceptible to the disease (S), those that are infected/infectious (I) and those that are either recovered or removed (R). The total population is then $N = S + I + R$. This model makes the assumption that once an individual has been infected they cannot be infected again and therefore it is unimportant whether individuals in the third category have recovered or have died. While the SIR model is very effective for describing the spread of many diseases, it is intended for large populations and is extremely unlikely to be accurate for the population in our model.

Instead the model used here is a stochastic one, which allows for much smaller populations. The two main factors looked at are the impact of varying different inputs (*e.g.* Death Rate, Meeting Rates, No. of Contacts) on the average number of possums dead and the time taken for half to die (of those that ended up dying). This covers both how far the disease spreads and how quickly it does so. The latter is defined as the time taken for half of those to die who will eventually die, as opposed to half of the total 40 possums.

2 Basic Model

Similarly to the SIR model, we assume that the population of N individuals can be divided into three subpopulations. The first contains those possums that are susceptible to the disease. At the beginning ($t = 0$) we are infecting only one individual, so the remaining $N - 1$ individuals fit into the susceptible category.

This one individual is the only one that is infectious (able to pass on the disease). We are assuming that once an individual is infected, it immediately becomes infectious. Each time an infectious individual comes into contact with a susceptible individual there is a fixed probability that the disease will be passed on. Since possums die from tuberculosis there is no chance that once one has been infected, they can become infected again. For the basic model we take the probability that an individual will die at any given time to be constant from the time of infection, and the same for every individual. At any given time, all N individuals should be contained within one of these three subpopulations (susceptible, infectious and removed).

Social Network - Matrix Representation

Tuberculosis is only able to passed on from an infectious possum to a susceptible possum through direct contact. These contacts can be represented in an $N \times N$ matrix where the possums are numbered 1 through N. The entries in the matrix represent the meeting rates (*e.g.* if the number where the 3rd row and 2nd column meet is a 5, then the 2nd and 3rd possums meet five times per time interval - the units of time in this model are unspecified). This matrix is symmetric: $R^T = R$ and there are no numbers along the diagonal as a possum is unable to 'meet' itself. Initially we

assume that each possum comes into contact with each of the other $N-1$ possums, and all of the meeting rates are equal.

For the purpose of this model we take death to be another possum, adding a column onto the matrix so that each possum also has a meeting rate with death. This rate is assigned once the possum becomes infected and remains constant. Each time an infected possum meets another possum there is a chance that it will be death. Once a possum is dead it is of course unable to meet anyone or become infected again.

Poisson Process

A poisson process is a stochastic process that measures occurrences of events. The number of these events occurring in a given time interval has a Poisson distribution. A Poisson process has the following four properties (Feldman and Valdez-Flores, 2010):

1. N(0) = 0 (the probability that zero events occur).
2. The intervals are independent (what happens in one time interval is not affected by events in any other time interval).
3. The number of events during a time interval is only dependent on the size of the interval, not on the timing of it.
4. Events cannot occur simultaneously.

Representing the contact network between the possums as a Poisson process means that the meetings between different possums are treated completely independently of each other.

This is possible because it has been shown that the rates of two or more separate poisson processes can be added together to give a total rate of events without changing the probability of any particular event occurring. For example, consider two different possum denning sites A and B. If den A is inhabited by a possum in average 3 times per week and den B is inhabited on average 2 times per week we are able to add these together and say that on average denning in this area occurs 5 times per week or every 1.4 days. Once it is determined when an event occurred we can then use the individual rates to determine what the event was (Daniel, 2008).

The time between successive events in a poisson process has been shown to have exponential distribution (Stewart, 2009). If R is the sum of the rates at which meetings between the possums occur then $1/R$ is the average time until a meeting will occur. Here we generate random numbers from an exponential distribution with mean $1/R$ to represent the time between successive meetings.

Results

Changing Death Rate

Figure 1 shows the spread of Tuberculosis through the basic model described. The simulation was run for low, medium and high death rates with all other variables held constant: All possums come into contact with each other possum 5 times per time interval, with a 50% chance of the disease being passed on if the meeting is between an infectious and susceptible possum. All three results show an initial short period of time in which the number of possums dead increases slowly. This is when there are very few possums infected and the disease is only beginning to spread. The

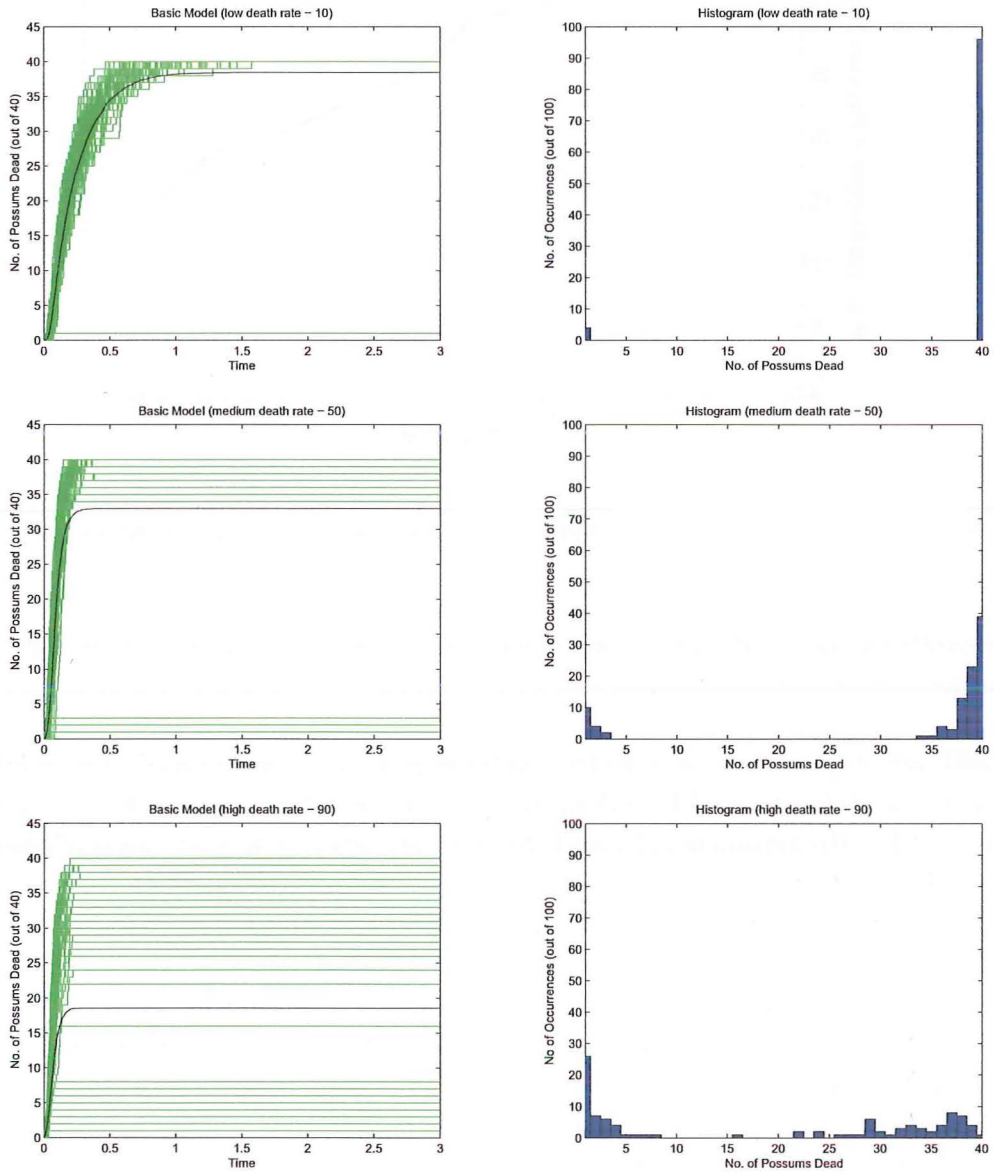

Figure 1: Results of Basic Model. The graphs on the left show the number of possums dead against time at three different death rates (green shows individual trials while black shows the average). The histograms on the right show the distribution of the final numbers dead.

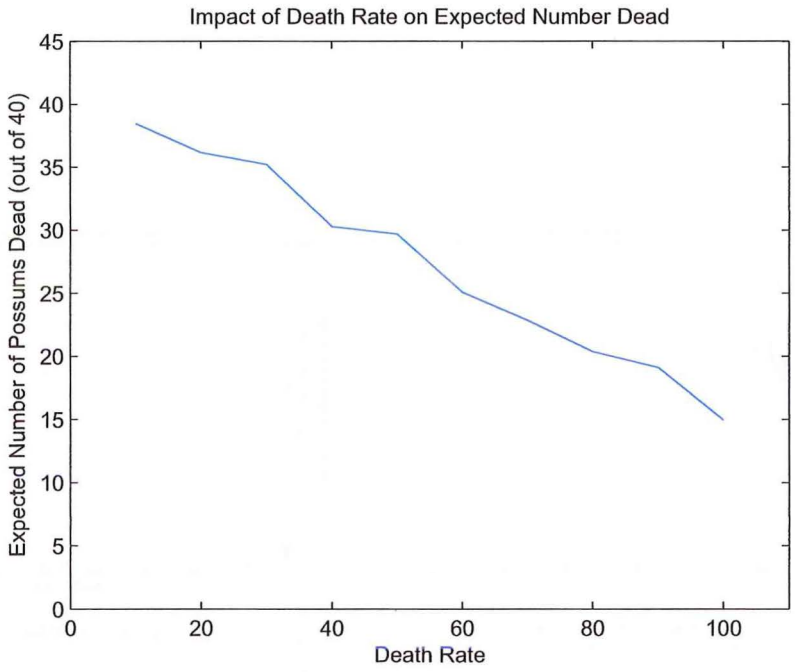

Figure 2: Change in the expected number of possums dead after the outbreak as the death rate is varied. All other variables are constant.

disease then spreads rapidly and the number of possums dead rises more quickly. As there are less possums remaining alive this increase slows and eventually stops.

As the death rate was increased the expected number of possums dying decreased. This is logical as there is a higher chance of each meeting being with death and therefore the infected possums have less of a chance to pass on the disease before they die. The histograms in Figure 1 show the distribution of the final number of possums dying at each death rate. At a low death rate this is generally all 40 possums with the occasional exception where the initial possum died before passing on the disease to anyone. The mean number dying here was 38.44 possums. At a medium death rate the expected number of possums dead decreased to 32.99 with lower numbers becoming more common. However, the histogram still only shows values less than 3 and greater than 34. The distribution of this appears to be similar to a bimodal distribution which has two distinct maxima instead of looking like a shifting normal distribution as may have been expected. Only at a high death rate is there a broader range of values (although high and low values are still more common) as the expected value decreases further to 18.56. Figure 2 shows a graph of the expected number of possums dead against the death rate. This has the same trend as in Figure One where as the death rate increases, the expected number of possums dying decreases. It shows a rather large decrease from the 38.44 at a death rate of 10, to only 14.97 at a death rate of 100. This decrease is reasonably uniform indicating a linear relationship.

From Figure 1 it also appears as if the entire process is occurring more quickly at higher death rates, as the slope evens out more quickly. This can also be seen in Figure 3, which shows the how the time taken for half of the possums to die changes as the death rate is increased (half of the number who eventually die, rather than half of the total population). Again this is expected as we are not changing the meeting rates. The disease is therefore still being passed on at a similar rate, however as the death rate increases less possums are dying in total (the value of the half is decreasing) because the infected possums are dying before passing it on. As there are less possums actually dying, the time taken for this to happen is also less. The trend here is no longer linear. Between a death rate of 10 and 20

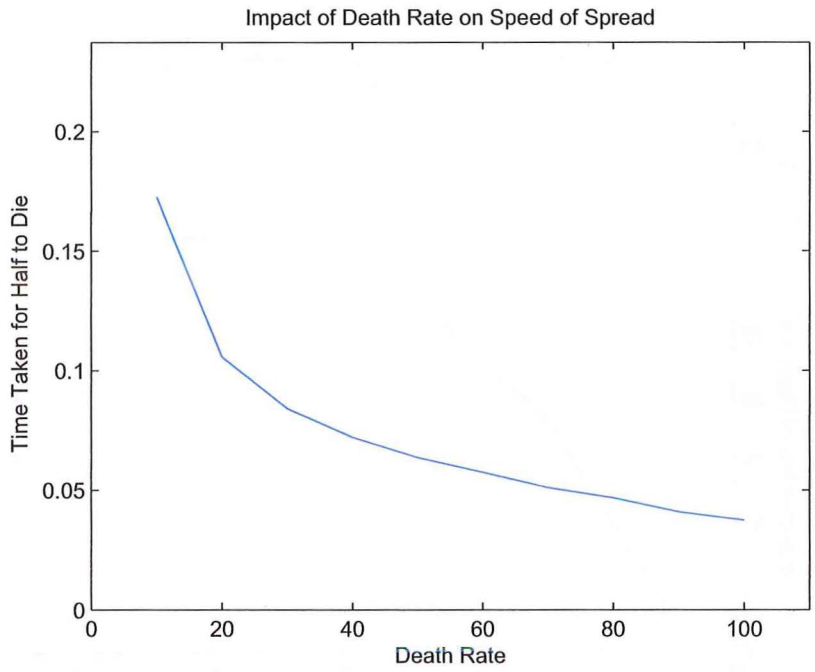

Figure 3: Change in the time taken for half of the possums to die as the death rate is varied. All other variables are constant.

the decrease is large, while after this all changes are much smaller.

Changing Meeting Rate

If we now look at the impacts of changing the meeting rate we get Figure Four and Figure Five below. These are similar to those above however they have a constant death rate of 50 (the medium death rate from Figure One) and a meeting rate varying between 1 and 10. This means that each possum is still coming into contact with all $N-1$ other possums but the frequency of these meetings is changing. In the previous results this meeting rate was 5.

Figure 4 shows the impact that this variation has on the expected number of possums dying. It has a strong increase between meeting rates of 1 and 5, and after this increases more slowly. In total the change is between 3.24 and 33.33 possums dying on average. As the frequency of meetings between possums increases, the disease is being passed on more quickly while the death rate remains the same. Therefore more possums in are becoming infected in total (and consequently more are dying). The change after a meeting rate of 5 is probably because the expected number dead is approaching the total of 40 possums. As we get even closer the slope will probably decrease further as it is not possible for more than 40 possums to die. We would expect the graph to have an asymptote at $y = 40$.

The impact of changes in the meeting rate on the time taken for half of the possums to die is shown in Figure 5. The graph shows a slight increase in the time as the meeting rate increase from 1 to 3, and after that a gradual decrease. The times taken are very similar between meeting rates of 1 and 10 (around 0.046) indicating that the meeting rate does not have any significant impact on the speed at which the disease spreads.

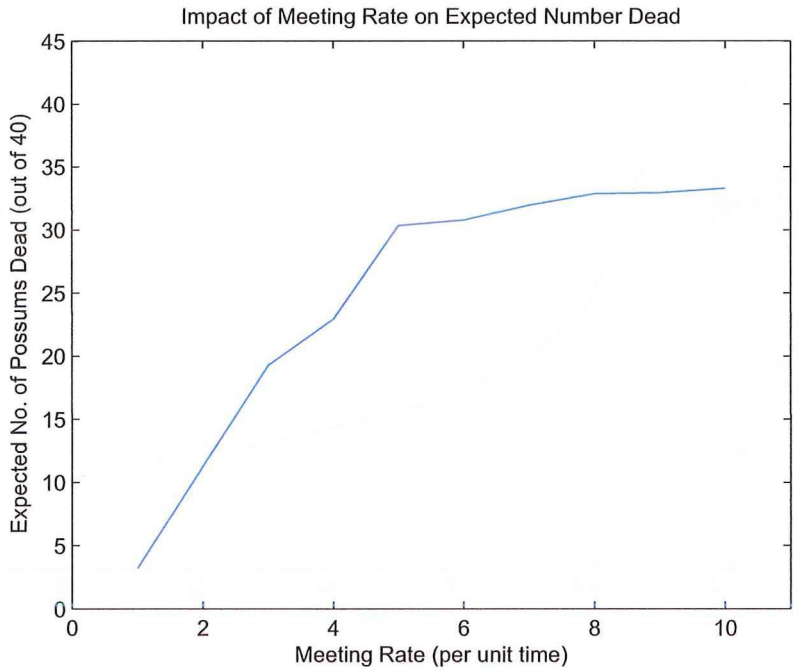

Figure 4: Change in the expected number of possums dead after the outbreak as the meeting rate is varied. All other variables are constant.

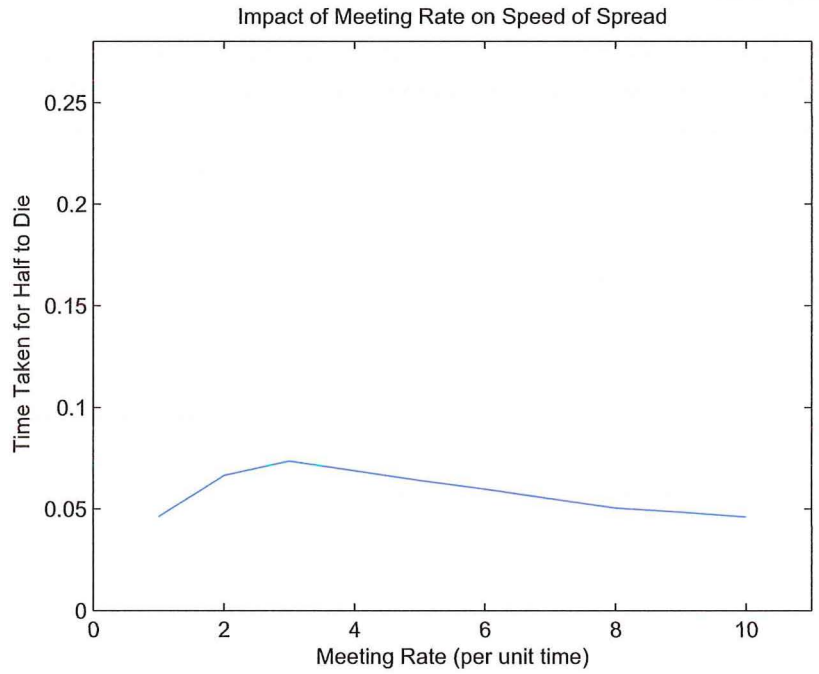

Figure 5: Change in the time taken for half of the possums to die as the meeting rate is varied. All other variables are constant.

3 Distributions

The previous results all assume that the possums meet with the same frequencies as each other, however this is not realistic. As with humans it is likely that there is great variation in how social individual possums are. In this section we use randomly generated numbers in the contact matrix so that instead of all possible meetings between possums occurring with the same frequency, there is some variation. The mean and variance of the meeting rates will still be the same for all possums. We can then hold each of these (mean and variance) constant while changing the other. In order for this to work the probability distributions we generate the values from need to give only positive values. The normal distribution would not work as it generates both positive and negative values. In this case we will look at the continuous uniform distribution and the gamma distribution. We would expect that changes to the mean would yield similar results to those obtained when the meeting rate was varied, as we are completing a very similar process.

Continuous Uniform Distribution

The uniform distribution takes parameters a and b with $a < b$, which are the bounds on the interval the values are able to come from. This gives a continuous random variable that has equal likelihood of taking on any value in the interval. The mean and variance of a random variable X with uniform distribution are (Stewart, 2009):

$$\mu = 1/2(a+b), Var[X] = 1/12(b-a)^2 \tag{1}$$

Gamma Distribution

The gamma distribution also has two parameters, α and β. α is the shape parameter as it changes the form of the density curve. β is called the scale parameter as it scales the curve both horizontally and vertically. The mean and variance of a random variable X with gamma distribution are as follows (Stewart, 2009):

$$\mu = \alpha\beta, Var[X] = \alpha\beta^2 \tag{2}$$

Results

Figure 6 and Figure 7 show the impact of variation in the mean meeting rates on the total number of possums dying, and the time taken for half to die respectively. The red lines show the results when the meeting rates are randomly generated numbers from a continuous uniform distribution and the blue lines show those from a gamma distribution. As before the death rate is set at 50, and the variance of the generated values is 1/3.

As expected both of these graphs strongly resemble those generated when varying the meeting rate in the previous section as we are making a very similar change. Again the expected number of possums dying increases sharply between mean meeting rates of 1 and 5 and then increases more slowly. The uniform distribution shows more of a variance in the expected number dead, with a sudden jump to 34.14 possums at a mean meeting rate of 6. The time taken for half of this process to happen again rises between mean meeting rates of 1 and 3 before gradually decreasing again to give a similar result at 10 to that at 1.

Figure 8 and Figure 9 show the same relationships with the variance of the randomly generated numbers being changed instead of the mean. The mean meeting rate here is set at 5, as the meeting rates were when we varied the death rate in the previous section.

In Figure 8 neither distribution appears to show a significant pattern. The expected number of possums dead is varying between 28.96 and 31.45 for the gamma distribution and 25.99 and 30.7 for the uniform distribution. There

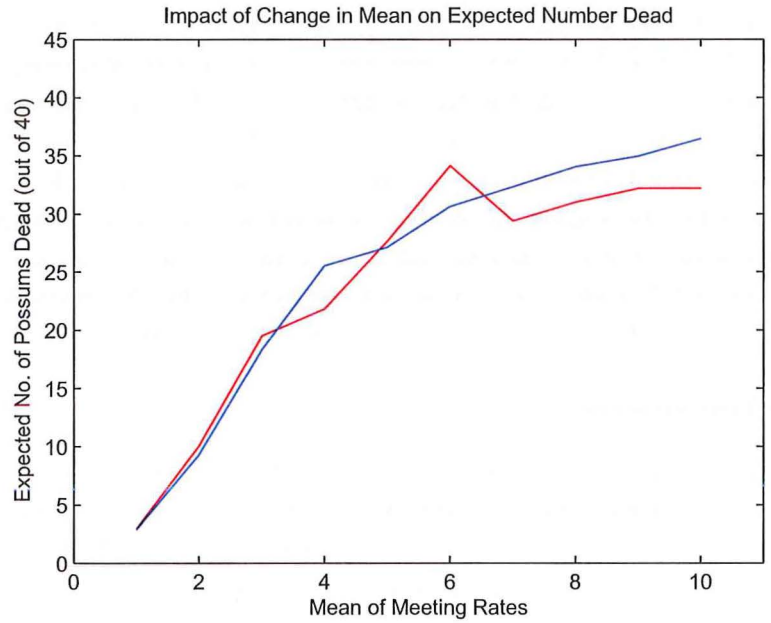

Figure 6: Change in the expected number of possums dead after the outbreak as the mean meeting rate is varied. All other variables are constant. Red shows the continuous uniform distribution and blue shows the gamma distribution.

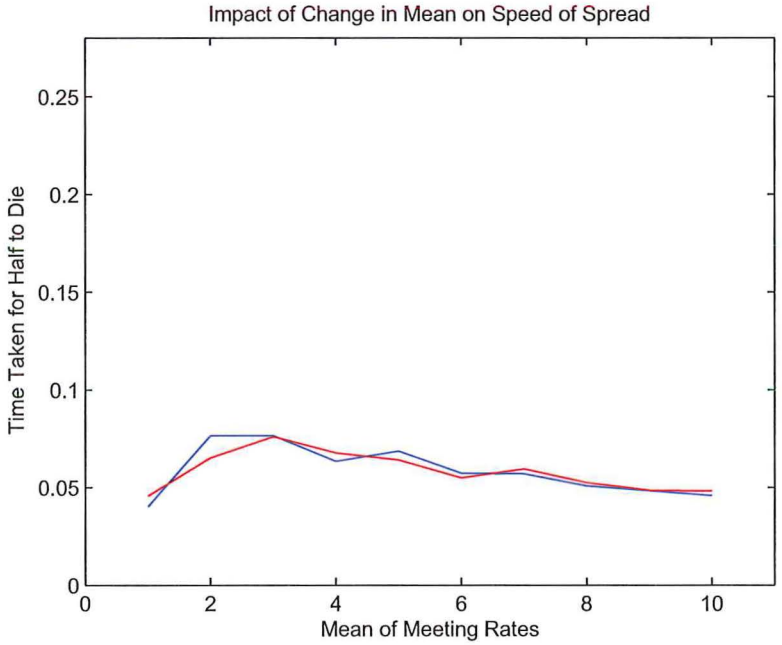

Figure 7: Change in the time taken for half of the possums to die as the mean meeting rate is varied. All other variables are constant. Red shows the continuous uniform distribution and blue shows the gamma distribution.

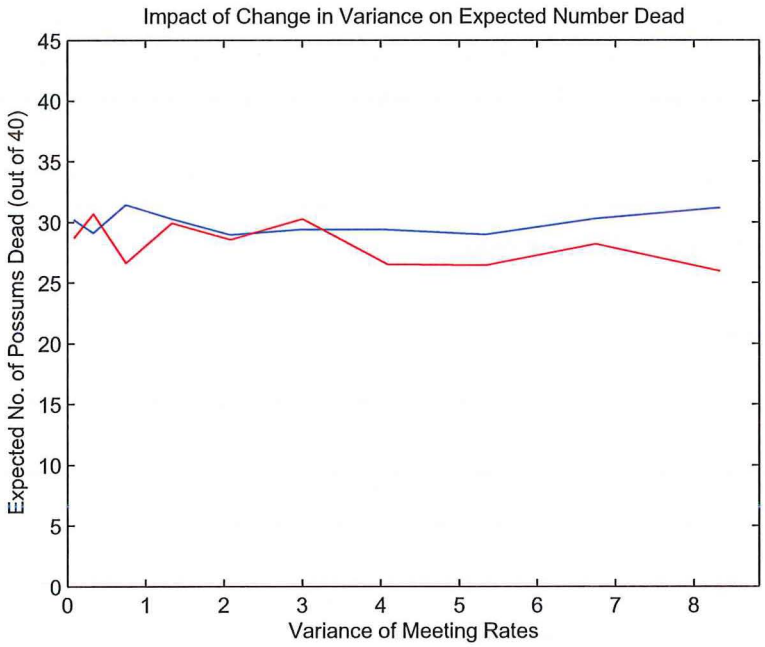

Figure 8: Change in the expected number of possums dead after the outbreak as the variance of the meeting rate changes. All other variables are constant. Red shows the continuous uniform distribution and blue shows the gamma distribution.

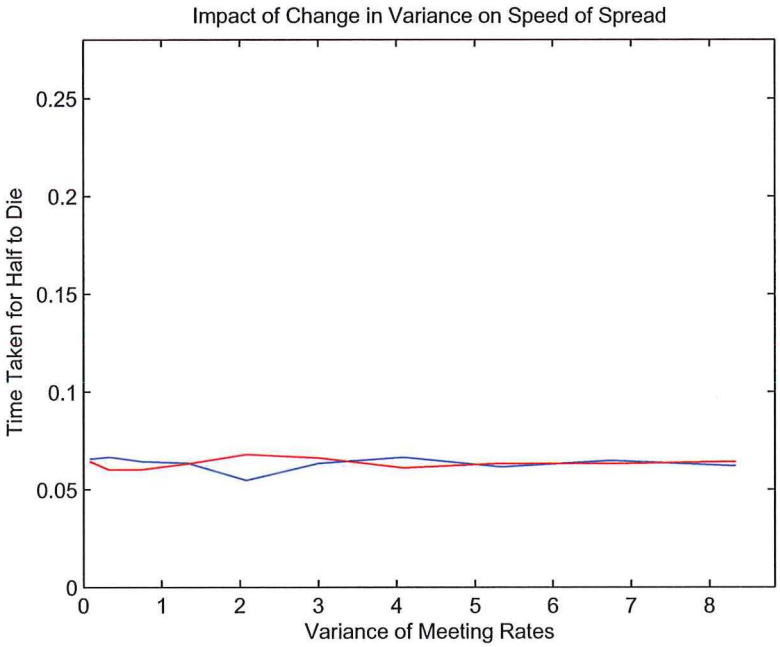

Figure 9: Change in the time taken for half of the possums to die as the variance of the meeting rate changes. All other variables are constant. Red shows the continuous uniform distribution and blue shows the gamma distribution.

appears to be a slight decrease for the uniform distribution as the variance is increased, but the gamma distribution does not show this. Figure 9 also shows little change in the time taken for half of the possums to die as variation changes. The difference between the minimum and maximum times taken here is only 0.013 whereas in Figure 3 it was 0.137. This is not a significant variation and there does not appear to be much of an increase or decrease.

All of these graphs shows very similar results for both the gamma and continuous uniform distributions which is to be expected they are using the same mean and variance. There is greater similarity between distributions in the time taken for half to die than in the expected number dead.

4 No. of Contacts

This model is still not very realistic as it assumes that each possums comes into contact with all $N-1$ other possums. Just as we do not meet everyone living in the same city or town as us, we cannot expect that a possum will have contact with every other possum inhabiting the same forest. This would assume a homogenous mixing of the population, which means that the number of contacts between possums is directly related to the population density (Smith, 2001). The method has been commonly used to model disease spread through populations however it is often not realistic as it does not cater for differences between individuals' social habits. As it is a fully connected network we would expect that which possum is infected should not have any significant impact on the spread of the disease (since the chance of an infectious possum passing on the disease is the same for everyone).

In this section we investigate the impact of changing the average number of contacts each possum has. This means that some of the entries in the matrix will be changed to zeros. While the number of other possums each one comes into contact with is changing, we adjust the frequency each time so that the total number of meetings occurring remains the same. When the number of contacts is the $N-1$ it was previously, the meeting rates are again 5. When the number of contacts is half of this, the meeting rates will be 10 so that the total number of meetings is still the same. Again we keep the death rate constant at 50. As the average number of contacts per possum decreases we would expect matrix properties to play a larger part. For example, when each possum has on average only one other contact there is a chance that the graph may not be fully connected. This would mean that there would be two or more separate groups of possums and if only one of these groups contained an infected possum there is no way that the disease could spread through the entire population. An example of this is the following 10×10 matrix with an average of one value in each row. This was randomly generated using the same method as in our model.

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 1 & 0 \end{pmatrix}$$

Rows 1, 4 and 8 have no values in them so these possums are not connected to anyone else in the network. Therefore the maximum number of possums that could contract the disease is 7, and if any of those three possums was chosen to

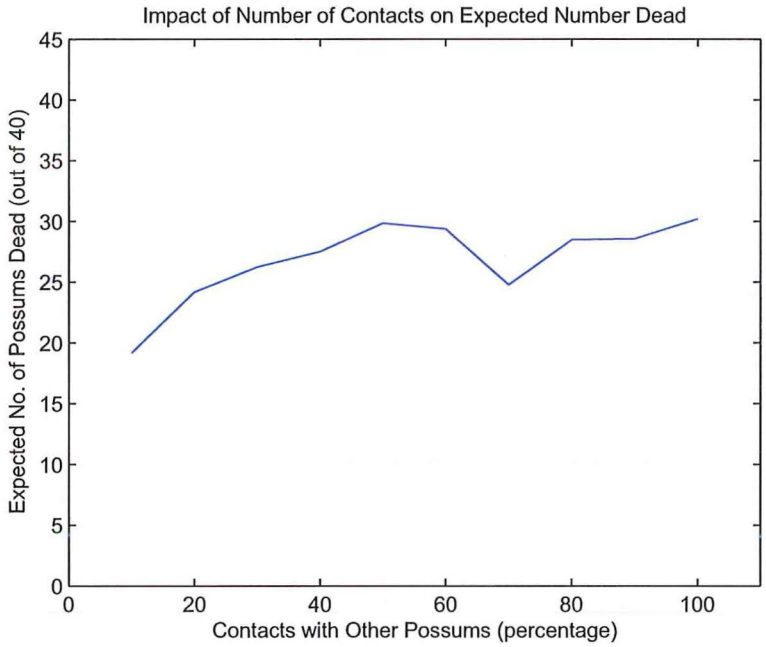

Figure 10: Change in the expected number of possums dead after the outbreak as the number of contacts each possum has changes. The average total meeting rate for each possum is still constant.

be infected initially they would not pass it on at all. This places more importance on which possum is initially infected.

Results

Figure 10 shows the impact of changing the number of contacts each possum has on the expected number that will die. The x-axis shows the percentage of the remaining 39 possums that each possum will on average have contact with. The trend shows an increase in the number of possums dying as the number of contacts they have increases from 10% to 100%. This line rises more steeply to begin with (between 10 and 50%) before appearing almost flat except for a sudden drop when the possums are coming into contact with 70% of the other 39. We would expect this increasing trend to be the case, as if an infected possum comes into contact with 39 other different possums the disease should spread more than if it only comes into contact with one other. At higher numbers of contacts this should not make as much difference as it is likely that the network is still fully connected and the disease will spread to most of the 40 possums.

The impact of the same changes on the time taken for half of the possums to die is shown in Figure 11. This shows an almost flat line so there is no obvious trend, which seems unusual as we would think that if the possum network was more connected we would see a decrease in the time taken. However, since there are less possums dying in total at lower percentages, it does seem logical that the process would not take significantly longer.

An important thing to note in these results is that the total number of meetings is constant, and it is only the number of different possums coming into contact with each other that changes. If the total number of meetings was not kept constant we would expect the results to reflect those from section one more closely where we changed the meeting rate.

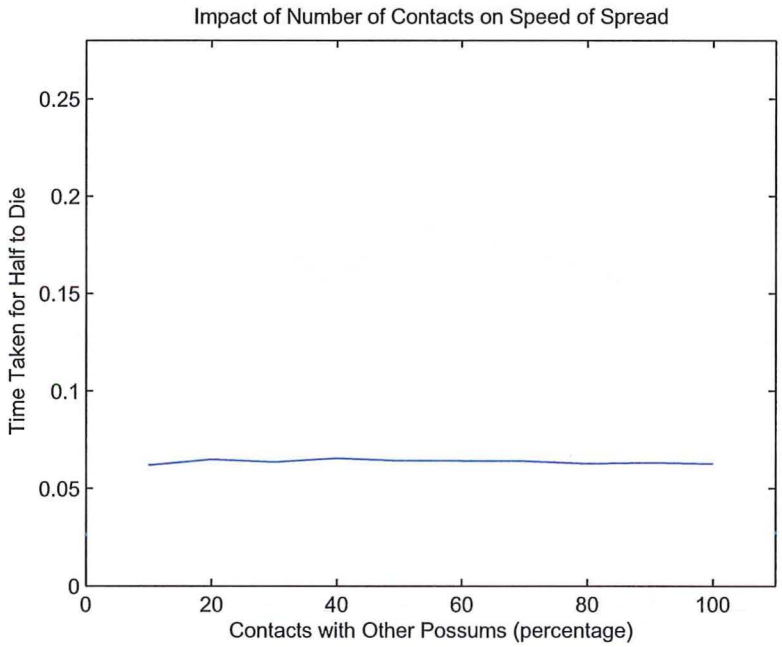

Figure 11: Change in the time taken for half of the possums to die as the number of contacts each possum has changes. The average total meeting rate for each possum is still constant.

5 Realistic Numbers

In this section we look at the results of the simulation if more realistic numbers are chosen. Here we assume that the possums meet another possum on average 25 times per year (Porphyre et al., 2008). The death rate here is simply set at 25 from the time of infection (giving the possums a 50% chance of dying initially).

Voronoi Diagram

A Voronoi diagram consists of points placed in a rectangular area. Each point has a corresponding cell consisting of all points whose distance from the point is not greater than their distance from any other point. It is obtained by drawing lines between the points and joining the midpoints of these lines. An example of this is shown in Figure 12 using 40 points. The contact rate between the possums in adjacent cells would then be represented by the length of the connecting line between them.

This particular diagram has an average number of edges per cell of 4.55. This would represent the average number of other individuals each of the 40 possums comes into contact with. We round this up to 5 so that each possum will come into contact with 5 other different possums. The individual meeting rates are therefore constant at 5 (total meetings per year / number of other possums in contact with).

If we run the simulation using these more realistic numbers we get the graphs in Figure 13. This shows very low numbers of possums dying when only one is infected initially (only 3.33 possums). This increased slightly to 11.81 when 5 possums were infected at the beginning as would be expected. Both processes are occurring within the time period of a year indicating that this would be a reasonable length of time to observe for.

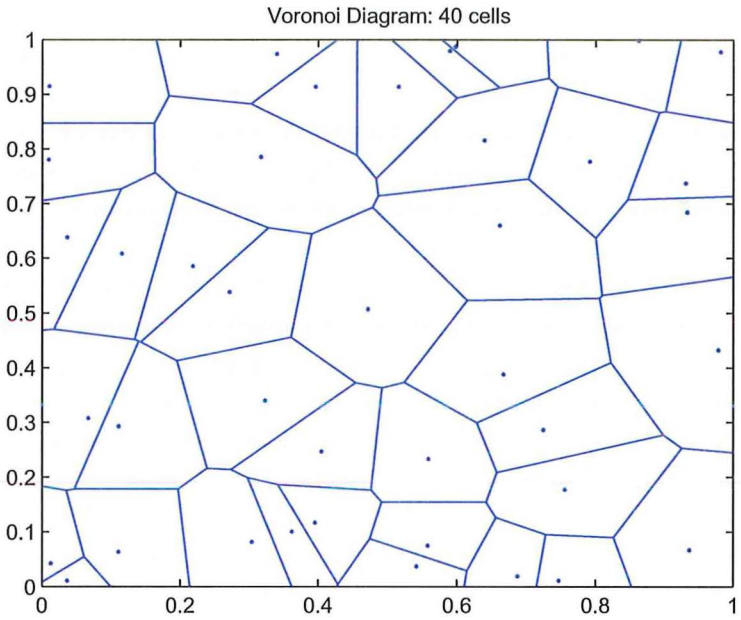

Figure 12: An example Voronoi diagram generated from 40 random points.

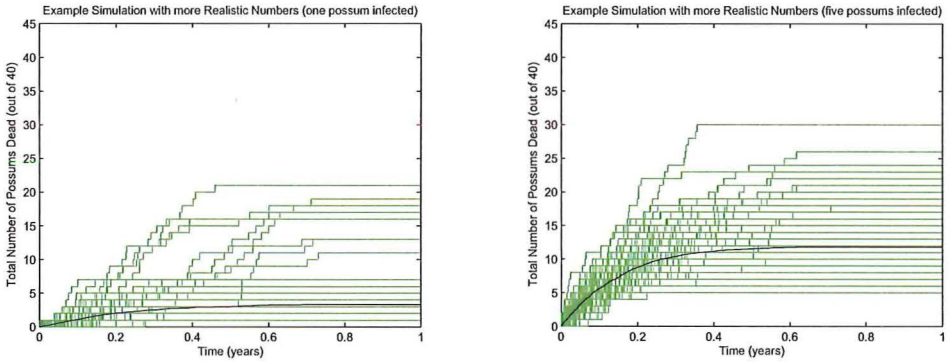

Figure 13: Example simulations using more realistic numbers with one and five possums initially infected respectively.

6 Discussion

We have looked at the impact of variation in 5 different factors on both the expected number of possums dying from tuberculosis and the time taken for half of this process to occur.

Our first result is that increasing the death rate of infected possums decreases both the number of possums becoming infected with tuberculosis (and consequently dying) because it does not have an opportunity to spread to the entire population, and also the time taken for this to occur. In this case the increase in speed is due to the possums dying more quickly as opposed to because the disease is actually spreading faster. As all other variables were held constant we find that as expected it is important to know the death rate for the infected possums.

We then looked at the impact of changing the meeting rate and found that at higher meeting rates, more possums are dying. This is likely to be because the chances of an infected possum meeting someone are now higher in comparison to the chance of dying, so the infection is spreading further through the population. The meeting rate does not appear to have a large impact on the speed of this process. As expected, when generating random meeting rates using the continuous uniform and gamma distributions, varying the mean of these rates gave extremely similar results. In all three cases there was initially a slight increase in speed between meetings rates of 1 and 3, which could be simply because the disease is spreading further before the infected possums die, as it corresponds to the largest increase in the expected number dying. While it is still the case at higher meeting rates that the disease has opportunity to spread further, once it is already affecting most of the population this is unlikely to make a significant difference.

Changing the variance of these randomly generated meeting rates but keeping the mean the same also gave very similar results for both distributions, however there appeared to be no significant trend. We conclude that the variation in meeting rates is not an important factor in this model provided that the mean is the same.

The final result we looked at was the impact of changing the number of other individuals an infected possum comes into contact with. As expected, the more different contacts an infectious possum has, the further the disease will spread, although again this increase is more notable at smaller values, perhaps because when most of the possums are becoming infected already it is not possible for the increases to be as large.

In conclusion, the important variables identified are the death rate, the mean meeting rates and the total number of other individuals each possum comes into contact with. If an experiment was being done with real possums, these would be the important things to observe before introducing the infection. It would then be possible to determine which possums were more social, and observe the difference between infecting possums with different social levels as Corner et al. (2003) has investigated.

When we looked at the simulation run with more realistic numbers we discovered that if only one possum was initially infected very little occurred and even with 5 initially infect only 11.81 were dying on average by the end of the simulation. Therefore in order for Dan to see anything significant in his experiments we would expect that he would need to infect more than one possum. We also found that the process was occurring within a year so therefore if he were to observe his populations for approximately that long after the initial infection he should get the results he is looking for. However, we have made the assumption that possum is able to die immediately after becoming infected which is not realistic.

7 Further Work

There are several different ways in which the models used in this project could be furthered or improved.

We have assumed a 50% chance that Tuberculosis will be passed on when an infectious possum and a susceptible possum meet. This is not very realistic for two reasons. Possums will have different rates of infectiousness and also different immune systems. Those with a weak immune system will be more likely to pick up tuberculosis than those with strong immune systems. This could be catered for by generating random numbers either for the infected possums' rate of passing on the disease or for the susceptible possums' rate of contracting it. It may create more variation in the total number of possums dying as if the initial possum infected has a very low infection rate then there is a greater chance that they will die before passing it on and vice versa.

Usually possums infected with Tuberculosis die about six months after developing signs of the disease (Landcare, 2000). Although the units of time in our model have not been specified, we have not specifically catered for this period of time. Instead the possums are able to die immediately after contracting the disease. It seems unlikely that the situations in which only 1 possum out of the 40 contracted the disease and died would occur if there was a delay between becoming infected and being able to die. If the units of time were known, a timer could be added to the model to calculate when 6 months has passed and the death rates only assigned for each possum once they have been infected for that length of time. It is also logical that as time passes the chance that a possum dies will increase. This would also ideally be catered for by increasing the death rate at certain times after infection.

Another factor that might be interesting to investigate is the impact of how connected the matrix is on the spread of the disease. This has been partially looked at in this project (Section Four) but not in great depth. As previously discussed if the matrix is not fully connected then only infecting one possum will mean that there is a subpopulation that is unable to contract the disease. This idea could be useful for determining the best control methods - whether it would be possible to isolate a subpopulation of possums with tuberculosis so that it cannot spread further.

Related to this is possum home range patterns, looking at different ways in which the matrix could be put together. If the population was able to be observed over an extended period of time it would be possible to actually determine approximate contact rates (as Dr. Tompkins is planning to do) however even without this information there are a couple of different methods by which the contact matrix could be made more realistic. Possums have their own home ranges and they are only going to come into contact with others where their home ranges overlap or meet. Consider an area of forest with 40 possums placed randomly. For simplicity we will assume this area to be rectangular. If we take these positions to be the center of the possums' home ranges we could then give each possum a circular home range and measure the overlap between adjacent circles. These overlaps would then form the numbers in the contact matrix. Alternately we could use the 40 random points to generate a Voronoi diagram as was briefly looked at in Section Five.

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